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ON IRREVERSIBLE EVOLUTION

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Evolutionary biology commonly addresses how and why organisms change. It also addresses how and why they do not change. Some types of change do not occur because of constraints—the evolution is simply prevented. The limitations on organic evolution are necessarily to be found at the levels of phenotypic variation, inheritance, and selection, just as the process of evolutionary change is also to be understood at these levels. Although some important constraints have already been discovered at these levels (e.g., inheritance is often Mendelian), further observations are needed in developing a comprehensive theory of evolutionary restrictions.

An extreme type of evolutionary restriction is irreversibility—the inability of a population to reacquire a (recent) ancestral state; this is sometimes known as Dollo's law (Simpson, 1953; Dobzhansky, 1970; Gould, 1970; see Discussion for a review). As a biological problem, irreversibility has two features distinguishing it from the much larger class of general evolutionary restrictions. First, irreversibility involves restrictions with respect to a

small set of phenotypes: the known ancestors. Second, since the unattainable phenotypes previously existed in the lineage, the restrictions result from the present characteristics of the population rather than from any intrinsic limitation of the species. Both of these features render irreversibility more amenable to analysis than evolutionary restrictions in general, and by developing a thorough understanding of irreversibility, insights to other classes of evolutionary restrictions may be obtained as a consequence.

This paper describes several phenotypic states that may exhibit evolutionary irreversibility. In acknowledging the existing literature on irreversibility, the analysis here differs from most previous treatments in two ways: i) The present examples are chiefly of genetic systems rather than morphological characters. ii) The underlying basis of irreversibility is identified from patterns of variation and selection—proposing *why* the transition to the ancestral state is unlikely—rather than inferring irreversibility from phyletic comparisons. Later in this paper we relax the requirement that the unattainable phenotypic states previously existed in the lineage and address a class of restricted transitions somewhat broader than strict irreversibility.

EXAMPLES

Seven possible examples of irreversible phenotypic states will be described below. Three cases will be described in detail to illustrate that the feasibility of evolutionary reversal is highly sensitive to the biological details of each system: parthenogenesis, polyploidy, and heteromorphic sex chromosomes. Four additional cases will be discussed briefly: Muller's ratchet, haplo-diploidy, selfing, and dioecy.

All-Female Parthenogenesis

All-female parthenogenesis (thelytoky) has evolved from sexual reproduction in a variety of animals (White, 1973; Maynard Smith, 1978; Bell, 1982). Certain types of thelytoky may be irreversible because they lack the variation to reacquire sexuality and because selection prevents the reversion. Two important changes usually accompany the evolution of thelytoky: the loss of males in the population, and a "meiotic" mechanism that maintains the same chromosome number in the egg as in somatic cells. The loss of males often has a simple explanation: if a sexual population is heterogametic in the male (XX female/XY male), the loss of males is equivalent to the loss of the Y, and males will not reappear until the Y (or an equivalent mutation) is reintroduced. The production of chromosomally unreduced eggs may have a variety of possible causes, ranging from i) chromosome doubling prior to meiosis, followed by two divisions with twice the usual number of chromosomes, ii) suppression of one meiotic division, or iii) completion of a normal meiosis, followed by fusion of two of the haploid nuclei (White, 1973; Bell, 1982).

The restoration of sexual reproduction in a thelytokous population requires two simultaneous events: fertile males must be introduced, and they must mate with females who produce "haploid" eggs when fertilized. The underlying genetic bases of maleness and of parthenogenetic meiosis are critical in the restoration of sexual reproduction. For example, if the origin of males requires a mutation in the form of an active regulatory gene, absent from females, males will arise only infrequently. Instead, if the origin of males merely requires the suppression of gene function on an X (as in XO males), males will arise frequently. Whether these males in turn produce successful offspring will depend on whether they mate with females producing reduced ova—a requirement automatically satisfied if the parthenogenesis is facultative, but dependent on further mutations if parthenogenesis is obligate. Therefore, obligate parthenogenesis is more likely irreversible than facultative parthenogenesis, but the nature of the mutations required to restore males is also important.

Thelytoky may also be irreversible because of stabilizing selection: models have shown that parthenogenesis is favored over outcrossing if the parthenogenetic offspring are more than half as fit as the outcrossed offspring (i.e., the "cost of meiosis," Williams, 1975, 1980; Maynard Smith, 1978; Bell, 1982; Uyenoyama, 1984). The same fitness requirements apply to the maintenance of parthenogenesis when it is common as apply to its invasion, so sexual reproduction is consistently selected against in parthenogenetic populations (subject to the limitations of these simple models).

The literature offers little direct empirical verification of the supposed irreversibility of obligate parthenogenesis. Males have been reported in some parthenogenetic species and have been found to be sterile. Some of these males were hybrids between a sexual species and the parthenogen, and they possessed one more set of chromosomes than the parthenogens (Bell, 1982). Thus, in support of the preceding arguments, these parthenogenetic females produced unreduced eggs even when inseminated.

Polyploidy

Polyploidy represents an increase in the number of chromosome sets transmitted per gamete and has commonly occurred in the evolution of plants. The evolution of certain types of polyploidy may be irreversible in sexual populations due to selection against the reversion, although low levels of polyploidy permit the evolution of higher levels (Stebbins, 1971, 1980).

To illustrate, consider a tetraploid derived from a hybrid of two species, with its tetraploid genome represented as G1G2/G1G2, where G1 (G2) is the haploid genome derived from species 1 (2). If the chromosomes of species 1 and 2 are sufficiently different, meiotic pairing will occur between each pair of G1 chromosomes and between each pair of G2 chromosomes, but not between G1 and G2

chromosomes. Gametes will be G1G2, and a diploid individual arising in this population would likely be G1G2, as if from an unfertilized egg.

Two factors militate against the evolution of the diploid. First, if it outcrosses, it will likely cross with tetraploids, and its offspring will be sterile triploids. This would have been a problem in the original evolution of the tetraploid, however, and it may be surmounted by selfing or other means (White, 1973). Second, the diploid may be sterile because of improper meiotic pairing, since it carries only one copy of each G1 chromosome and G2 chromosome. This latter complication is more important in allopolyploids than in autopolyploids, since the genomes of allopolyploids are derived from different races or species, whereas the haploid genomes of autopolyploids are all derived from one population.

In plants, the reversion to diploidy from tetraploidy may also be selected against because of gene expression in the gametophyte (e.g., pollen). In higher plants, especially angiosperms, the limited evidence available suggests that a large fraction of the genes are expressed during the haploid gametophytic phase (Tanksley et al., 1981). The evolution of tetraploidy changes the gametophyte from a haploid to a diploid and is accompanied by a gradual but major increase in the frequency of recessive deleterious mutations among genes expressed in the gametophyte. Reversion from a diploid to a haploid gametophyte may then be disadvantageous because any recessive deleterious genes in the pollen can no longer be masked by wild-type alleles and will therefore be expressed (cf. Crow and Kimura, 1970 pp. 316–317).

Many botanists have regarded polyploidy as irreversible, at least when the polyploid's chromosome sets are distinct enough that each chromosome has only one true homologue, as in many allopolyploids (Stebbins, 1971, 1980; Raven and Thompson, 1964; de Wet, 1971). Raven and Thompson (1964) first challenged the conventional wisdom that all types of polyploidy were irreversible, and de Wet actually selected a reversal from tetraploidy to diploidy (referred to in de Wet, 1971, 1980), but such reversals seem difficult and may be restricted to recently evolved autopolyploids.

Heteromorphic Sex Chromosomes

Heteromorphic sex chromosomes are the cytological manifestations of many XX/XY sex-determining mechanisms in plants and animals. They sometimes prevent the evolution of new mechanisms lacking heteromorphism (Bull, 1983 pp. 82, 246–247). Heteromorphic sex chromosomes (X and Y) are generally regarded to have evolved from an initial state of cytological similarity or "homomorphism," in which the genetic differences between the X and Y were confined to one or a few loci. Following the suppression of X-Y crossing over, X-Y differences began to accumulate, with the Y chromosome losing many of its functions, accu-

mulating heterochromatin, and becoming reduced in size (Muller, 1914; reviewed in Darlington, 1937; Ohno, 1967; Bull, 1983 Chap. 16). X chromosomes have apparently maintained most of their original functions, although new functions have been acquired in some cases (e.g., dosage compensation, whereby the X-linked genes are regulated differently than the autosomal genes).

The X-Y differences that accompany extreme heteromorphism may prevent the loss of heteromorphism. Heteromorphism is lost only when a new sex-determining mechanism evolves, whereupon both sexes become XX or both become YY. However, YY individuals cannot survive without an X once the Y has degenerated. In addition, XX males are sterile in some species (although there are many others in which XX males are fertile). The combination of YY inviability and XX male sterility, then, prevents the loss of heteromorphism. Both XX male sterility and YY inviability have been observed in mammals and *Drosophila*, and these restrictions readily explain why the sex chromosome systems are highly conserved within each taxon (reviewed in Bull, 1983; the conserved nature of the mammalian X was first noted by Ohno, 1967).

Muller's Ratchet

Muller (1964) noted that a genome or chromosome which never recombines is subject to a special accumulation of deleterious mutations in a finite population: without recombination, the genome "can never get to contain, in any of its lines, a load of mutations smaller than that already existing in its present least-loaded lines." Thus if the lowest number of deleterious mutations per genome in a population is regarded as a phenotype, this phenotype cannot revert to an ancestral state of fewer mutations. The lowest class at any one time can be lost, however, and the ratchet moves forward. The existence and importance of this ratchet process has no direct empirical support, but it appears to be an inevitable consequence of systems without recombination (see discussions by Charlesworth, 1978; Maynard Smith, 1978; Bell, 1982).

Haplo-Diploidy (Arrhenotoky)

A genetic system common among arthropods is haplo-diploidy, in which males arise from unfertilized eggs, females from fertilized eggs, and which has likely arisen from normal diploid systems (Bull, 1983 Chap. 11). Two properties of haplo-diploidy render it unlikely to revert to diploidy. i) Since males are haploid in the germ line, they require a special meiosis. The appearance of fertile diploid males thereby requires a modification in sex determination coincident with a modification in spermatogenesis to accommodate diploidy; either effect alone is eliminated from the population. ii) Haplo-diploidy is advantageous to the mother from the "cost of meiosis" principle described above for parthenogenesis: a haploid son transmits maternal genes at twice the frequency per gamete relative to a bipa-

rental (diploid) son; hence, females are favored to produce haploid sons even if diploid sons are fertile (Bull, 1983 Chap. 12). Evidence for the irreversibility of haplo-diploidy along the lines of (i) comes from the Hymenoptera (ants, bees, wasps), in which viable diploid males—which arise occasionally as a consequence of a peculiar sex-determining mechanism—are sterile because they produce diploid sperm (reviewed in Bull, 1983 Sec. 11.C).

Selfing

The evolution of complete selfing in a hermaphroditic population may be irreversible because of a genetic advantage stemming (again) from the cost of meiosis (Lande and Schemske, 1985). In an outcrossed population, selfing is often disadvantageous because inbred progeny suffer "depressed" fitness relative to outcrossed progeny. In the absence of severe inbreeding depression, however, selection favors selfers over outcrossers (Fisher, 1941; Maynard Smith, 1978; Lloyd, 1979; Charnov, 1982; Lande and Schemske, 1985). Inbreeding depression is apparently due to largely recessive, deleterious genes maintained by mutation; if selfing begins to evolve, the frequencies of these deleterious genes are greatly reduced, inbreeding depression is lessened, and the advantage of selfing is intensified (Lande and Schemske, 1985). The little empirical evidence from plants bearing on this model was discussed by Schemske and Lande (1985).

Dioecy and Hermaphroditism

The evolution of dioecy from hermaphroditism may be irreversible, especially after dioecy has been maintained for many generations. Even though males and females in most dioecious species possess nearly equivalent sets of genes, the simultaneous expression of genes for male and female phenotypes may lead to detrimental consequences rather than to a functional hermaphrodite. For example, the hormonal basis of secondary sex differences in vertebrates may prevent an individual from being functionally male and female simultaneously (cf. Adkins-Regan, 1981). There is, in fact, abundant evidence from many dioecious animals that, although individuals with characteristics of both sexes arise at moderate frequencies, functional hermaphrodites are extremely rare (for gynandromorphism in insects and birds: Metz [1938], Bacci [1965], Crew [1965]; hermaphroditism in frogs: Witschi [1929]; in birds: Witschi [1961], Crew [1965], Miller [1938], Masui [1967], Frankenhuis [1977]; in mammals: Ohno [1979], Austin and Edwards [1981], McLaren [1981], Bull [1983]). (An ancestry of hermaphroditism is at best remote in these cases, but the point of interest here is that the transition from dioecy to hermaphroditism is apparently precluded.)

DISCUSSION

This paper offered several examples of evolutionary irreversibility, attempting to explain why, in each case, the formerly ancestral state is unattainable. The concept of evolutionary irreversibility has an old and well-established precedent under the name Dollo's law (thoroughly reviewed by Gould, 1970). Most generally, Dollo's law proposes that the full range of phenotypes of an organism never reverts exactly to an ancestral condition; in this sense, the law describes the improbability of retracing history rather than restrictions on evolution. Dollo's law is also used in the narrower sense as the principle of evolutionary reduction: lost morphological structures are usually not regained (also known as Abel's law and Meyrick's law), and in this sense the law may indeed reflect restrictions on change, although the extent to which this law is valid remains controversial (Meyrick, 1884; Simpson, 1953; Rensch, 1954; Brown, 1965; Crowson, 1970; Dobzhansky, 1970; Gould, 1970; Salthe, 1972; Henig, 1979; Wagner, 1982; Minkoff, 1983).

Comparisons among previous studies and the present one highlight three differences regarding the inference used to identify irreversibility as well as the classification of irreversibility. i) The examples of irreversibility here were identified from an understanding of the processes governing the evolutionary transitions in each case, in contrast to the usual practice of identifying irreversibility from phyletic comparisons, i.e., by noting merely whether particular reversions do in fact occur. ii) The present treatment limited its examples to those represented by an evolutionary pattern—a phenomenon repeated independently in several taxa (as also in Strathmann [1978], Stebbins [1974 pp. 149–151], and the systematists' principle of evolutionary reduction described above [Brown, 1965]). Thus, the uniqueness of history does not contribute to the irreversibility. In contrast, some interpretations of Dollo's law incorporate the uniqueness of history as a basis of irreversibility (cf. Simpson, 1953; Crowson, 1970; Salthe, 1972; Wagner, 1982; Minkoff, 1983). iii) The present and some previous treatments (e.g., Strathmann, 1978; Stebbins, 1974) addressed irreversibility at a defined phenotypic level, regardless of mechanisms at other levels (and regardless of effects on population survival/extinction—cf. Simpson's [1953] blind alleys and evolutionary traps). For example, if the ability to digest cellulose was the defined phenotype, loss of this ability would be irreversible under the present analysis only if cellulose digestion (in any form) could not be regained. Instead, various forms of Dollo's/Abel's/Meyrick's law would not regard the reacquisition of cellulose digestion as reverse evolution if, for example, the enzymatic basis of the new system differed from that of the old (Meyrick, 1884; Rensch, 1954; Crowson, 1970; Dobzhansky, 1970; Wagner, 1982). (Minkoff [1983] described an early controversy of this nature regarding the interpretation of Dollo.) It remains an open question as to what levels are most appropriate in the analysis of irreversibility.

In light of the foregoing points (ii) and (iii), the

present examples offer a more general description of restricted evolution than does strict irreversibility: if the evolution of state B from state A is irreversible, then the transition from B to A should be prevented, regardless of whether A was an ancestor of B. For example, the transition from dioecy to hermaphroditism should be difficult for dioecious species with an ancestry of hermaphroditism, as well as for dioecious species with other ancestries. In the discussion that follows, therefore, we address irreversibility in this broader sense.

Generalities from the Examples

A striking feature of the examples here is the extreme dependence on underlying mechanisms. For example, the reversibility of parthenogenesis may vary greatly depending on the genetic bases of males and of parthenogenetic ovogenesis; similarly detailed considerations apply to many other cases of irreversibility. Therefore, do any generalities emerge? It can generally be anticipated that irreversibility results from constraints imposed at the levels of selection, inheritance, and phenotypic variation. In some examples, clear selective bases of irreversibility were identified: polyploidy, parthenogenesis, haplo-diploidy, and selfing (the "cost of meiosis" being the selective force in the last three cases). For Muller's ratchet, irreversibility was due simply to lack of variation. In most cases, however, irreversibility was due to a combination of constraints imposed at the levels of selection and variation.

Two generalities emerge from the analysis, although they are somewhat superficial and do not readily lead one to predict a priori other cases of irreversibility. 1) Selection of intermediate phenotypes is critical to evolutionary transitions whenever the two phenotypes (A and B, say) are so different that multiple mutations are required to change from one to the other. Even if A is favored over B, A will not evolve from B if the intermediate phenotypes are disadvantageous. This principle may apply to four of the above cases of irreversibility: parthenogenesis, sex chromosomes, haplo-diploidy, and dioecy. While random effects in small populations can sometimes overcome disadvantageous intermediates in the evolution of new adaptive states (e.g., Wright's [1977 Chap. 13] shifting balance theory), the intermediates in the present examples are so disadvantageous that they are not likely to be overcome even under the circumstances most favorable to genetic drift.

When intermediate phenotypes are involved in changing from one character state to another, it may not seem obvious why a transition is easier in one direction than in the other. Three reasons for irreversibility are suggested (assume that evolution proceeds from A to B but not the reverse). First, the origin of B from A may involve degradation of genes necessary for A; it is generally easier to destroy gene function than to create it. Second, the origin of B in a population of A may require fewer mutational changes than the origin of A in a population of B: the loss of males during the evolution of parthenogenesis is a consequence of selection, whereas establishing males in a parthenogenetic population may require a mutation. Third, the intermediates may be subject to directional selection, so that the transition from A to B is favored regardless of the initial population.

2) A second principle common to several examples is that the genome may progressively "accommodate" a character state the longer it is maintained. The mere persistence of one state in a population may select or permit changes that are compatible with it rather than with alternative states, and the longer a state persists, the greater the difficulty for the evolution of alternative states (i.e., historical constraints; Muller, 1939; Dobzhansky, 1970). Dioecy provides the clearest example: ever-increasing specializations of males and of females may eventually lead to the point that both phenotypes cannot successfully function in the same individual. A corollary of accommodation is that disuse of a function may permit its degeneration. Consequently, the loss of a major phenotype may permit the loss of structures and functions that were dedicated to its support (with some examples suggested in Goldschmidt [1940 pp. 362–363], Williams [1975 p. 169], and Whittaker [1979]). This corollary may apply to several of the above examples—parthenogenesis, haplo-diploidy, sex chromosomes, and especially to the irreversibility of lost morphological structures (the usual examples of Dollo's/Abel's/Meyrick's law).

A knowledge of irreversibility, or more generally, restricted transitions is important for at least three reasons. First, irreversibility represents a form of restricted evolution, and the identification of restrictions provides a useful complement to studies describing causes of evolutionary change. Second, in systematics studies, the prior knowledge of restricted transitions facilitates the construction of cladograms (Farris, 1977; Felsenstein, 1979). Third, an awareness of irreversibility and other forms of restricted transitions is essential when using comparative methods of testing evolutionary hypotheses. For example, consider the hypothesis that hermaphroditism is expected to evolve in sessile organisms (Charnov et al., 1976). One test of this hypothesis is to compare the incidence of hermaphroditism among sessile species with its incidence among mobile species. However, if hermaphroditism were sometimes prevented from evolving in a dioecious population, dioecy would occasionally be observed in the settings expected to favor hermaphroditism (Charnov, 1982).

In conclusion, seven possible examples of irreversible genetic systems have been described here: parthenogenesis, polyploidy, heteromorphic sex chromosomes, Muller's ratchet, haplo-diploidy, selfing, and dioecy. Based on these examples, the existence of irreversible evolution seems fundamentally dependent on the biological details of each

particular system, but some generalities may apply at a superficial level.

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WHY DISTASTEFUL BUTTERFLIES HAVE APOSEMATIC LARVAE AND ADULTS, BUT CRYPTIC PUPAE: EVIDENCE FROM PREDATION EXPERIMENTS ON THE MONARCH AND THE EUROPEAN SWALLOWTAIL

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Warning coloration has long been regarded as a means by which distasteful animals gain increased protection against predators by announcing their noxious properties (Bates, 1862; Cott, 1940). Since it has commonly been assumed that i) individual predators have to learn to avoid aposematic prey, and that ii) aposematic prey are killed when handled by predators, kin selection has been considered a prerequisite for the evolution of aposematic coloration (Fisher, 1930; Benson, 1971; Wilson, 1975; Harvey and Greenwood, 1978; Krebs and Davies, 1981). In this context it is relevant to point out that Guilford (1985) has argued that kin selection has often been invoked erroneously in the above argument, and should not be confused with a second but distinct effect of family grouping (see also Harvey et al., 1982). Both processes, however, describe the spread of a phenotype with indirect benefits. As a consequence we will recognize "indirect selection" as the alternative to individual selection for the evolution of aposematic coloration.

We have shown that the majority of a variety of aposematic insects actually survive being handled by birds (Järvi et al., 1981a; Wiklund and Järvi, 1982), thus forcing us to conclude that the evolution of aposematic coloration is possible by means of individual selection (Järvi et al., 1981a; Wiklund and Järvi, 1982; Sillén-Tullberg and Bryant, 1983). Generally, if a distasteful prey could not survive predator attacks we should regard indirect selection as necessary; otherwise, individual selection could be a sufficient explanation for this type of coloration.

A review of butterfly faunae from different parts of the world (Ford, 1945; Shirozu and Hara, 1960–1962; Common and Waterhouse, 1972; Howe, 1975) reveals the pattern that the larval and adult stages of distasteful species are often aposematically colored, whereas the pupae are cryptic.

In this paper, using hand-raised Japanese quails *Coturnix coturnix* as predators, we show that the aposematic larvae and adults of the monarch *Danaus plexippus* and the European swallowtail *Papilio machaon*, respectively, can survive attacks, where-